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## Denning phenology and reproductive success of wolves in response to climate signals

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3 1 *Running head: Climate signals in wolf denning phenology*

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5 2 ***Title: Denning phenology and reproductive success of wolves in response to climate signals***

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1  
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3 37 *Abstract (300 words)*

4 38 Arctic and boreal ecosystems are experiencing rapid changes in temperature and precipitation  
5 39 regimes. Subsequent shifts in seasonality can lead to a mismatch between the timing of resource  
6 40 availability and species' life-history events, known as phenological or trophic mismatch.  
7 41 Although mismatch has been shown to negatively affect some northern animal populations,  
8 42 longer-term impacts across large regions remain unknown. In addition, animals may rely on  
9 43 climate cues during preceding seasons to time key life history events such as reproduction, but  
10 44 the reliability of these cues as indicators of subsequent resource availability has not been  
11 45 examined. We used remote sensing and gridded spatial data to evaluate the effect of climate  
12 46 factors on the reproductive phenology and success of a wide-ranging carnivore, the gray wolf  
13 47 (*Canis lupus*). We used GPS location data from 388 wolves to estimate den initiation dates (n =  
14 48 227 dens within 106 packs) and reproductive success in eight populations across northwestern  
15 49 North America from 2000-2017. Spring onset shifted 14.2 days earlier, on average, during the  
16 50 18-year period, but the regional mean date of denning did not change. Preceding winter  
17 51 temperature was the strongest climatic predictor of denning phenology, with higher temperatures  
18 52 advancing the timing of denning. Winter temperature was also one the strongest and most  
19 53 reliable indicators of the timing of spring onset. Reproductive success was not affected by timing  
20 54 of denning or synchrony with spring onset, but improved during cooler summers and following  
21 55 relatively dry autumns. Our findings highlight a disconnect between climate factors that affect  
22 56 phenology and those that affect demography, suggesting that carnivores may be resilient to shifts  
23 57 in seasonality and yet sensitive to weather conditions affecting their prey at both local and  
24 58 regional scales. These insights regarding the relationship between climate and carnivore  
25 59 demography should improve predictions of climate warming effects on the highest trophic levels.

30 60 *Keywords*

31 61 reproduction, *Canis*, canid, carnivore, demography, trophic mismatch  
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## 1. Introduction

Phenological responses to climate are pervasive in the natural world (Stenseth and Mysterud 2002, Thackeray *et al* 2010, 2016). Annual cycles characterized by changes in temperature, precipitation, and hydrology can drive temporal patterns in nutrient availability and resource distribution, with profound effects on habitat suitability (Parmesan 2006, Chen *et al* 2011), species demography (Regehr *et al* 2007, Inman *et al* 2012, Stirling and Derocher 2012), and community composition (Walther *et al* 2002, Henry and Molau 2003, Ovaskainen *et al* 2013). Individuals that time resource-limited life history events to coincide with peak resource availability should accrue fitness benefits relative to those who do not (Parker *et al* 2009, Boutin and Lane 2014, Thackeray *et al* 2016, 2010). Thus, the consequences of phenological asynchrony with optimal conditions due to changing environments is a major conservation concern. The demographic repercussions of phenological mismatch have been documented for several wildlife species at lower trophic levels (Miller-Rushing *et al* 2010, Thackeray *et al* 2010), but the impacts of climate variability on large carnivores are not well understood. The fundamental role of large carnivores in shaping communities suggests this deficiency may limit our understanding of how future climate change will impact community stability and species viability (Miller-Rushing *et al* 2010, Wilmers *et al* 2012, Winnie and Creel 2017).

Weather may signal changes in resources vital to reproduction. Reproduction is likely sensitive to weather conditions due to the considerable increase in energy requirements associated with offspring development and in some cases, post-parturition parental care (Ofstedal and Gittleman 1989). Reproduction often requires preparatory actions, both behavioral (e.g., courtship) and physiological (e.g., dormancy, incubation, and gestation), that can create a temporal disconnect between climate signals at the onset of reproduction and resource pulses around the time of parturition (Gienapp *et al* 2014, Both *et al* 2009). Thus, the ability to match optimal conditions for rearing offspring may reflect selective pressures acting on breeding phenology and fitness following parturition (Kerby and Post 2013). In seasonal systems where optimal conditions are ephemeral, the abiotic environments that are within the physiological tolerances of neonates and that affect the temporal variability in prey availability, vulnerability, and predictability are likely to affect the extent to which carnivore reproductive phenology responds to climate signals (Inman *et al* 2012, Gienapp *et al* 2014, Both *et al* 2009).

Although some species may adjust their timing of parturition in response to weather cues, the degree of seasonality and magnitude of cross-seasonal correlations in weather are likely to influence the predictability of resource pulses (Colwell 1974) and therefore, the extent to which species respond to climate cues. If seasonal conditions are highly correlated (e.g., mild winters associated with mild springs, or early autumns associated with early springs), species may modify breeding phenology in response to climate cues during the breeding season that signal optimal weather conditions for parturition or offspring development. If seasons are weakly correlated, then climate cues during the breeding season would be unreliable indicators of the climatic state during the offspring rearing period, and species would not be expected to adjust timing of breeding in response to weather variability. To examine the potential value of breeding season conditions as indicators of offspring rearing conditions, we examined inter-seasonal correlations in weather during our 18-year study period. We also examined whether the level of inter-seasonal correlation has changed over time to determine whether previously strong climate indicators are breaking down with climate change.

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3 106 Here, we examined the influence of climate on gray wolf (*Canis lupus*) reproduction from 2000-  
4 107 2017. As one of the most well-studied and widespread apex predators, gray wolves are an ideal  
5 108 candidate for investigating climate drivers in carnivore reproduction. With an extended gestation  
6 109 of approximately nine weeks ( $62 \pm 3$  days), wolves breed in the winter and give birth in the  
7 110 spring with a high degree of synchrony across social units (i.e., packs) within populations (Asa  
8 111 and Valdespino 1998, Mech and Boitani 2010). Although very little is known about the  
9 112 underlying mechanisms associated with the timing of wolf reproduction, the synchrony in spring  
10 113 parturition, as well as the observed delay in parturition at higher elevations (Joly *et al* 2018) and  
11 114 latitudes (Mech and Boitani 2010), indicate strong selective pressures acting on wolf denning  
12 115 phenology with possible cuing by climate signals. Therefore, we evaluated potential climate  
13 116 mechanisms underlying two components of grey wolf reproduction using a large regional dataset  
14 117 from North America (table 1 & 2). We specifically assessed whether prior environmental  
15 118 conditions influenced the timing of natal den initiation (i.e., phenology), and whether past or  
16 119 contemporary environmental conditions influenced reproductive success (i.e., presence of one or  
17 120 more pups at the end of August) in wolves. Our findings pertaining to the effects of climate on  
18 121 the demography of wolves will likely have important implications for numerous sympatric  
19 122 species worldwide.

## 23 123 **2. Materials and Methods**

### 24 124 *2.1 Study domain*

25 125 We compiled GPS location data from 388 individuals in eight wolf populations across western  
26 126 Canada and Alaska (fig. 1)(Longitude: -154.6 to -112.7°, Latitude: 51.5 to 67.8°; table 2).  
27 127 Wolves were captured following standard animal care protocols defined by affiliate university or  
28 128 government agencies and released with Global Positioning System (GPS) collars programmed to  
29 129 acquire fixes over a range of intervals from 15 minutes to 24 hours. Each population was  
30 130 monitored from one to 12 years between 2000-2017.

### 33 131 *2.2 Wolf denning phenology & reproductive success*

34 132 The movements and site-fidelity patterns of resident pack members can signal pup-rearing  
35 133 activities from March through August (Alfred en 2006, Tsunoda *et al* 2009). These patterns  
36 134 emerge from food provisioning and other social interactions that regularly draw pack members  
37 135 back to pup-rearing sites that serve as social centers throughout the summer (i.e., dens and  
38 136 rendezvous sites) (Alfred en 2006, Ballard *et al* 1991, Ciucci and Mech 2006). Thus, the  
39 137 movements of non-reproductive individuals can be as informative as reproductive individuals  
40 138 (Tsunoda *et al* 2009).

43 139 We classified movements indicative of pup rearing using a three-step process. For the first step,  
44 140 we identified sites with a high-intensity of use by clustering collared animal locations in space  
45 141 ( $\leq 100$  m) and time ( $\leq 7$  days) (R package rASF (Mahoney and Young 2017)). This process is  
46 142 performed iteratively over all locations within an animal's truncated time series, producing  
47 143 convex hulls for each set of points that meet the criteria. We then merged all overlapping convex  
48 144 hulls (in space and time) into a single cluster and removed any clusters with fewer than eight  
49 145 locations (or five for 24-hr fix interval datasets). For the second step, we smoothed the same  
50 146 movement time series using a median filter and an overlapping, 4-day moving window to  
51 147 dampen the effect of large movements. We flagged 4-day periods with median daily  
52 148 displacements less than 200 meters and overlaid the output on our cluster data. For the final step,  
53 149 we visually inspected movement time series to evaluate whether cluster fidelity persisted after  
54 150 frequent offsite forays (i.e., provisioning of offspring) and to identify any influential gaps in

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3 151 location data that could affect estimates for den initiation dates (fig. 2). We estimated parturition  
4 152 as the initial date from the earliest denning cluster observed during the reported period for wolf  
5 153 parturition (March – June; Mech and Boitani 2010). Occasionally, movement data from a  
6 154 reproductive female expressed gaps in a location time series that lasted approximately four to  
7 155 eight days, an indication of GPS satellite signal occlusion while in underground dens (Joly *et al*  
8 156 2018). Visual inspection of the time series helped to identify these gaps so that den initiation  
9 157 dates (i.e., parturition dates) could be adjusted to when the signal was first lost. However, in  
10 158 cases where denning initiation were unclear, particularly for known non-breeding individuals,  
11 159 the movement data were removed from further consideration.

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14 160 We define reproductive success as packs with one or more pups at the end of August. To  
15 161 estimate success, we evaluated the movement time series for each individual after a denning  
16 162 event had been identified. If pup-rearing movements were evident through the end of August  
17 163 using the same methods above (e.g., high-fidelity clusters and low daily median displacement  
18 164 through August), we flagged these packs as reproductively successful. Although these activities  
19 165 often extended well into September or October, we chose August as a more conservative date  
20 166 given the variability in when pups begin to consistently travel with natal packs. We validated  
21 167 success by comparing our estimates to visual observations of pups with packs during the autumn  
22 168 or winter for a portion of our dataset for which these observations were made (Denali National  
23 169 Park and Preserve, Banff National Park, Jasper National Park, and West Athabasca River study  
24 170 areas).

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27 171 In addition, because we performed these assessments for each individual independent of pack  
28 172 membership, we used pack members as a form of validation in our estimates for both den  
29 173 initiation and reproductive success. However, for the analyses below, we used only one estimate  
30 174 of reproductive timing and success per pack per year, prioritizing dates derived from  
31 175 reproductive females followed by individuals with the highest quality data (i.e., highest fix  
32 176 retention or sampling rate).

### 33 177 2.3 Climate metrics

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35 178 We aggregated seasonal weather metrics using Daymet (v3; Thornton *et al* 2018), a  
36 179 meteorological product that contains daily estimates for minimum and maximum temperatures,  
37 180 total precipitation, and snow water equivalent (SWE) on a global one-kilometer grid. To  
38 181 characterize vegetation dynamics during the most photosynthetically active periods (i.e., growing  
39 182 season), we estimated Normalized Difference Vegetation Index using 8-day surface reflectance  
40 183 derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS; MOD09Q1  
41 184 data product, ORNL DAAC 2017). We post-processed NDVI data using the program TIMESAT  
42 185 (Jönsson and Eklundh 2004), which masked cloud covered pixels, smoothed NDVI time series,  
43 186 and estimated phenological metrics such as start of growing season (SOS), length of growing  
44 187 season (LOS), and time-integrated NDVI (tiNDVI). We defined growing season start and end  
45 188 dates by when pixels passed the 10% and 90% thresholds for mean NDVI amplitude as measured  
46 189 across a seasonal time series. We estimated snow disappearance date (SDD), or the first snow  
47 190 free day after a minimum of 3 days with snow cover (assessed backwards in time to capture the  
48 191 end of the snow-covered season), using the MODIS normalized snow difference index  
49 192 (MOD10A1; Hall *et al* 2006) and the Google Earth Engine API. We also included PDO  
50 193 (<http://jisao.washington.edu/pdo>; Mantua and Hare 2002) and Arctic Oscillation indices (AO)  
51 194 (NOAA National Weather Service Climate Prediction Center; <http://www.cpc.ncep.noaa.gov>)

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3 195 during January of the reproductive year and annual means from the previous year (effectively, a  
4 196 lag of one year; fig. 3b). See table 3 for a complete description of each covariate.

6 197 To define local domains for weather conditions, we calculated seasonal wolf home ranges using  
7 198 95% isopleths from fixed-kernel density estimates (Sheather and Jones 1991). We defined three  
8 199 biological seasons: summer (pup-rearing: April - August), autumn (ungulate rut: September -  
9 200 November), and winter (wolf pair formation and breeding: January - March). We used seasonal  
10 201 home ranges to extract median climate statistics, and home range centroids to estimate latitude  
11 202 for each individual. In the absence of wolf movement data during any non-denning seasons,  
12 203 summer home ranges summaries were used instead given the strong seasonal site fidelity  
13 204 exhibited by wolves (Mech and Boitani 2010).

#### 16 205 *2.4 Analyses*

17 206 Prior to the analyses, we assessed collinearity across all covariates and removed one or more  
18 207 covariates that contributed to correlation coefficients greater than 0.7. In cases where correlation  
19 208 occurred, we retained the metric that best represented the underlying, hypothesized biological  
20 209 mechanisms.

22 210 We also evaluated temporal trends in median SOS and denning date during the years for which  
23 211 we had wolf denning data by fitting linear mixed effects model with either SOS or denning date  
24 212 as the response variable, a single continuous effect of year, and random intercepts for study  
25 213 system. We estimated shifts in dates based on predictions derived from models with significant  
26 214 effects of year (95% confidence interval for year did not overlap zero).

29 215 Next, we evaluated inter-seasonal correlations (fig. 1). We defined population domains by their  
30 216 minimum convex polygons (MCP; Calenge 2006) using all collared individuals within a  
31 217 population. For each population domain, we estimated median SOS, seasonal temperatures,  
32 218 cumulative precipitation, and SWE across all years within the study (2000-2017). We then  
33 219 generated population-specific Pearson's correlation coefficients by pairing SOS with climate  
34 220 metrics from the previous winter, autumn, and summer during each year, thus producing annual  
35 221 estimates of correlation for each climate metric by population across all years.

37 222 We used a time-to-event model, Cox proportional hazard regression (R package survival,  
38 223 Therneau 2015), to examine the effects of climate factors on denning phenology. Denning  
39 224 phenology was measured as the number of calendar days since January 1st and the initiation date  
40 225 of each documented denning event. The baseline 'hazard' in this context reflected the daily  
41 226 probability of denning from January through the middle of June. We derived robust, Huber  
42 227 sandwich variance estimates to account for non-independence in the timing of denning for packs  
43 228 with more than one denning event across multiple years (i.e., specified 'cluster(PackID)' in the  
44 229 model formulation; Therneau 2015). We evaluated the influence of seasonal (previous summer,  
45 230 autumn, and winter) minimum and maximum temperatures, previous summer and autumn  
46 231 cumulative precipitation, mean daily SWE, SDD, SOS, LOS, tiNDVI, latitude, annual PDO, and  
47 232 annual AO on the timing of wolf den initiation.

51 233 We assessed climatic factors affecting reproductive success using mixed logistic regression with  
52 234 success (1) and failure (0) as a binary response (R package lme4; Bates 2010). We included  
53 235 random intercepts for pack nested within population and evaluated the influence of synchrony  
54 236 with spring onset (i.e., the difference between denning date and start of growing season), annual  
55 237 PDO (previous year), seasonal weather conditions, and time-integrated tiNDVI. In contrast to the  
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phenology analyses, summer conditions were based on the current reproductive year rather than from the previous summer. In addition to a linear effect of spring onset, we considered a non-linear second-order polynomial and a linear piecewise response to synchrony with spring onset (i.e., using a single knot at 0 representing perfect synchrony) to account for possible differences in success whether litters were born before or after spring onset. We also included summer home range area (km<sup>2</sup>) as an indirect measure of home range quality, because smaller home ranges are often associated with higher resource productivity (Duncan *et al* 2015).

We standardized all covariates by centering on the mean and dividing by one standard deviation prior to modeling (Gelman *et al* 2014). We ran all-possible additive models using the R package MuMIn (Barton 2009). Models were ranked by Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). We generated model-averaged coefficient estimates and confidence intervals based on unconditional standard errors following Burnham and Anderson (2002). Model-averaged coefficient estimates were derived across all models, but the estimate for any particular covariate was conditional on its presence within a model (i.e., coefficients were not fixed at 0 when absent). We determined variable importance using parameter weights (Burnham and Anderson 2002) and confidence interval overlap with zero (85% level; Arnold 2010). We also evaluated both model sets for uninformative parameters using personally authored R code (*sensu* Leroux 2019), which we retained when deriving parameter weights (to achieve covariate balance across model sets; Burnham and Anderson 2002) and model-averaged estimates in an all possible models context (Arnold 2010).

We assessed model goodness-of-fit by using the Cox proportional hazard concordance statistic for the denning phenology model set (Therneau 2015) and conditional pseudo-R<sup>2</sup> for the reproductive success model set (Nakagawa *et al* 2017). Concordance is a measure of agreement between observed and predicted values commonly used in time-to-event models (Therneau 2015). This is accomplished by ranking the ‘risk’ scores (exponentiated linear predictor in a hazard model) of a pack at each observed denning event relative to all packs who have yet to den. Values of zero correspond to the lowest ‘risk’ of denning relative to the remaining packs (i.e., poor predictive ability); whereas, values of one correspond to the highest ‘risk’ of denning (i.e., perfect predictive ability). Concordance is then estimated as the weighted average of these rankings across all denning events, with values approaching one indicative of stronger predictive accuracy.

### 3. Results

#### 3.1 Denning summary

We compiled movement data from 388 wolves and identified 227 possible dens associated with 106 packs across western Canada and Alaska between 2000 and 2017. Of these, we classified reproductive success for 186 reproductive events in those packs with sufficient movement data (i.e., data from denning through the end of August and  $\geq 1$  fix per day). Although rare, we treated multiple litters as a single event based on the timing of the first den and any pup-rearing movements through August as a single measure of success. Validations comparing our movement-based predictions to aerial and ground observations of denning indicated that we successfully identified 100% of the known denning events ( $n = 146$  known dens). We had two or more collared individuals for 41 of these dens, permitting us to calculate variation in estimated den date across individuals of different sex and breeding status. The median difference was 1 day ( $\mu = 1.95$ ,  $SE = 0.31$ , range = 0 to 8 days).



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3 282 Of 153 confirmed aerial or ground observations of recruitment (i.e., packs with or without pups  
4 283 after August 31st of each year), 143 cases matched our predictions of success (93.5%). Of the ten  
5 284 misidentified, six were estimated as failures but observed to be successful and three were  
6 285 estimated as successful but observed to be failures. Thus, error in recruitment classification was  
7 286 relatively minor without, we believe, inducing any systematic bias associated with the ‘type’ of  
8 287 error due to near equal representation. We corrected the ten misidentified reproductive success  
9 288 estimates to reduce the overall classification error rate in our data set.

### 12 289 *3.2 Inter-seasonal climate correlations: Summer, autumn, winter correlations with SOS*

13 290 Autumn and winter mean temperatures were negatively correlated with start of growing season  
14 291 (Autumn:  $r_{\text{mean}} = -0.50$ ,  $\text{SE} = 0.07$ ; Winter:  $r_{\text{mean}} = -0.40$ ,  $\text{SE} = 0.05$ ) and did not show a trend  
15 292 over the 18-year period for which we had data (2000 – 2017) (fig. 4). Summer temperature was  
16 293 also negatively correlated with SOS ( $r_{\text{mean}} = -0.57$ ,  $\text{SE} = 0.09$ ) but demonstrated a slight trend  
17 294 toward weaker correlation in recent years. Summer and winter precipitation, as well as winter  
18 295 SWE, showed slight but highly variable correlations with SOS and no apparent temporal trend  
19 296 (fig. 4). However, autumn precipitation exhibited a temporal trend, switching from positive to  
20 297 negative correlation during the same 18-year period.

### 23 298 *3.3 Denning phenology*

24 299 The estimated median denning date was May 4 ( $\text{SD} = 13.6$  days), on average 14.7 days prior to  
25 300 the start of season. SOS advanced an average of 14.2 days from 2000 to 2017, whereas the  
26 301 median denning date did not change (fig. 3a & S1). As expected, denning was initiated earlier at  
27 302 lower latitudes, but variability in the timing of denning occurred among all populations. Latitude  
28 303 was strongly correlated with seasonal temperatures (e.g., Winter  $T_{\text{max}}$ :  $r = -0.77$ ), as was SOS and  
29 304 SDD ( $r = 0.83$ ). Because effects of latitude and SDD were largely accounted for by the other  
30 305 climate variables (fig. S2), latitude and SDD were removed from further consideration in this  
31 306 analysis. Further, we limit our discussion to seasonal maximum temperatures because of  
32 307 consistent model interpretations and generally improved model fit over minimum temperatures.  
33 308 Approximately 18.1% of phenology models expressed some degree of uninformative covariates  
34 309 (Leroux 2019). When present, these covariates consisted of LOS (5.5%), SOS (2.3%), autumn  
35 310 precipitation (4.3%), summer precipitation (3.7%), and autumn temperature (2.3%), which were  
36 311 consistent with relatively low parameter weights for these covariates (table 5). Models with  
37 312 evidence of uninformative covariates did not appear in our top models (table 4).

41 313 The best model ( $\Delta\text{AICc}$  relative to Null = -43.52; Concordance = 0.67,  $\text{SE} = 0.02$ ) for denning  
42 314 phenology included winter and summer maximum temperatures, tiNDVI, annual PDO, and  
43 315 autumn precipitation in order of support via parameter weights (table 4 & 5). In general, denning  
44 316 occurred earlier in regions or years with warmer temperatures during summer and winter seasons  
45 317 preceding parturition. However, denning was delayed following years with higher tiNDVI and  
46 318 PDO, as well as with higher precipitation in autumn and winter (table 5). Importantly, our results  
47 319 may indicate that wolf reproductive phenology was responding to photoperiod, or latitude as a  
48 320 proxy, rather than winter temperatures (Asa and Valdespino 1998). Although statistically  
49 321 intractable due to a strong correlation between latitude and winter temperature, we included an  
50 322 additive effect of latitude within our best reproductive phenology model to evaluate how the two  
51 323 metrics were confounded. Notably, the model maintained significant effects for winter ( $\beta = 0.25$ ;  
52 324  $\text{SE} = 0.13$ ) and summer temperatures ( $\beta = 0.27$ ;  $\text{SE} = 0.09$ ), but estimated a non-significant  
53 325 effect for latitude ( $\beta = -0.20$ ;  $\text{SE} = 0.15$ ). Though qualitative, this result would indicate there was  
54 326 some redundancy between temperature and latitude (i.e., photoperiod), but that seasonal

327 temperatures were capturing additional variation independent of latitude; therefore, temperatures  
328 were more informative drivers of phenology at both regional and local population levels.

### 329 *3.4 Reproductive success*

330 The best model for reproductive success included autumn precipitation, summer maximum  
331 temperatures during pup-rearing, annual PDO, and home range area (in order of support via  
332 parameter weights) ( $\Delta AICc = -15.85$  relative to the null model;  $R^2 = 0.22$ ; table 5). Model-  
333 averaged coefficient estimates indicated pup recruitment through the end of August increased  
334 significantly with positive PDO during the previous year and declined with increased autumn  
335 precipitation, increased summer maximum temperatures during the current pup-rearing season,  
336 and increased home range area (table 4 & 5; fig. 5). We found no support for a linear effect,  
337 second-order polynomial, or a linear piecewise response to synchrony with spring onset (with a  
338 knot at perfect synchrony). The piecewise analysis allowed testing for differences in  
339 reproductive success whether animals denned early or late relative to the mean difference  
340 between den date and SOS. The confidence intervals for both piecewise coefficients overlapped  
341 0 ( $\beta_{<0} = -0.23$ ,  $CI_{95} = -1.05$  to  $0.59$ ;  $\beta_{>0} = 0.21$ ,  $CI_{95} = -0.42$  to  $0.84$ ), indicating no difference in  
342 the influence of phenological match on reproductive success between cases where denning  
343 occurred early or late relative to SOS. Approximately 35.1% of success models expressed some  
344 degree of uninformative covariates (Leroux 2019). When present, these covariates consisted of  
345 annual AO (13.0%), autumn temperature (10.2%), winter temperature (5.4%), match with SOS  
346 (3.2%), summer precipitation (2.6%), and tiNDVI (0.7%), which were also consistent with  
347 relatively low parameter weights for these covariates (table 5). Models with uninformative  
348 covariates did not appear in our top models (table 4).

## 349 **4. Discussion**

350 Species' phenological responses to climate change have garnered significant research interest in  
351 recent years (Aubry *et al* 2013, Post and Forchhammer 2008, Thackeray *et al* 2016). Only a few  
352 of these studies have established a mechanistic link between demography and phenological  
353 match with optimal conditions and highlighted the costs to survival or reproductive success of  
354 being too early or too late (Rode *et al* 2018). Here, we identified a disconnect between climate  
355 factors signaling denning phenology from those that influenced reproductive success in gray  
356 wolves. Although warming temperatures have advanced spring start of growing season by  
357 approximately two weeks in less than two decades in our study region, both the timing and  
358 success of reproduction were insensitive to spring advancement despite sensitivity to seasonal  
359 conditions. These findings highlight that changes in the timing and magnitude of environmental  
360 conditions may each have distinct effects on species as climate change continues.

361 The gestation period of many mammals creates a temporal disconnect between breeding and  
362 offspring birthing seasons. Thus, climate cuing is likely most effective at signaling future  
363 climatic states (e.g., during parturition) in cases where such cues are strongly correlated with  
364 desirable environmental conditions at the time of the phenological event. Understanding how  
365 correlated, and therefore effective, these cues are through time can provide important insights  
366 into how climate change might be expected to influence species phenology. Here, given the  
367 adherence to spring parturition in wolves, we found that winter temperature was the best and  
368 most consistent predictor of both spring onset and denning phenology, with the lowest  
369 interannual variability and no temporal trend in correlation strength during the 18-year study  
370 period. However, previous summer temperature was also a strong predictor of wolf denning  
371 phenology, but may be a less reliable indicator of spring onset due to declines in correlation in

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3 372 recent years. These differences in the reliability of climate signaling highlight the importance of  
4 373 understanding which cues plant or animal populations may be using to time key life history  
5 374 events, and may be an underappreciated factor explaining variable responses among species to  
6 375 climate change.

8 376 As with many temperate carnivores, wolves exhibit a high degree of synchrony and seasonal  
9 377 fidelity in parturition phenology. Such seasonal birth cycles are likely indicative of climate-  
10 378 driven, temporal patterns in resource availability (Oftedal and Gittleman 1989), defined broadly  
11 379 as the abiotic conditions conducive to neonate survival (Russell *et al* 2002), the availability of  
12 380 materials needed for reproduction (e.g., den construction; Liston *et al* 2016, Rode *et al* 2018), or  
13 381 food for reproducing females and/or developing young (Regehr *et al* 2007, Inman *et al* 2012,  
14 382 Stirling and Derocher 2012). We found that wolf denning phenology was most responsive to  
15 383 local climate cues during the winter breeding season, with cooler winters delaying spring  
16 384 denning and parturition. Although winter temperature was an important predictor of denning  
17 385 phenology, wolves within our region did not respond to year-to-year variation in the start of  
18 386 growing season (or snow disappearance date), nor was their reproductive success sensitive to  
19 387 synchrony with spring onset. In addition, spring onset advanced approximately 14 days during  
20 388 the period from 2000 to 2017 across all populations. Although trends in SOS vary considerably  
21 389 at high latitudes and throughout the Arctic (e.g., 5.3 to -18.9 days • decade<sup>-1</sup>; Zeng *et al* 2013),  
22 390 our estimated rate of SOS advancement are in-line with those reported for other regions of the  
23 391 Arctic during a similar time period using remote sensing (e.g., 4.5 to 5.1 days • decade<sup>-1</sup> in  
24 392 Alaska's National Parks; Swanson 2017) and from ground observations (e.g., Greenland: 10 days  
25 393 from 2000 to 2013; Westergaard-Nielsen *et al* 2017). Yet, there was no statistical change in  
26 394 mean denning date across all populations over the same period (similar to Joly *et al* 2018). These  
27 395 patterns suggest that variation in the availability of spring denning habitat as defined by climatic  
28 396 suitability is not a limiting factor for wolves. Given the reproductive synchrony and adherence to  
29 397 spring denning within wolf populations, however, such insensitivity to interannual variation in  
30 398 spring onset may indicate wolves are responding to spring conditions at coarser temporal and  
31 399 spatial scales.

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37 400 Indeed, the importance of PDO, a regional climate index, was evident in both denning phenology  
38 401 and success, suggesting wolf reproductive ecology is broadly responsive to regional climate  
39 402 patterns at time scales longer than a year. We chose PDO as a predictor because of its strong  
40 403 influence in the Arctic-boreal region of western North America, and large ungulate population  
41 404 dynamics specifically (Hebblewhite 2005, Hegel *et al* 2010a, Post and Forchhammer 2002). For  
42 405 our populations, positive annual PDO was associated with warmer winters, earlier start of  
43 406 growing season, and reduced winter precipitation in those populations experiencing the deepest  
44 407 snowfalls (fig. S3). Our results indicated regional warm and dry cycles (i.e., larger PDO) delayed  
45 408 timing of denning the following year (notably, CIs indicated non-significance by 0.01), opposite  
46 409 of both temperature and precipitation effects at local levels. Wolf parturition could be delayed in  
47 410 response to increases in prey populations that often occur during positive PDO cycles  
48 411 (Hebblewhite 2005, Hegel *et al* 2010a, Joly *et al* 2011) because higher densities may reduce  
49 412 maternal body condition, increase gestation length, and lead to delayed parturition in many of the  
50 413 ungulate species that wolves prey upon in the region (Cameron *et al* 1993, Singer *et al* 1997,  
51 414 Keech *et al* 2000). Reproductive phenology of large carnivores should correspond to prey  
52 415 phenology, whether peak parturition or timing of migration (Klaczek *et al* 2015), and the extent  
53 416 to which wolves respond to climatic conditions may depend upon the scale and magnitude of a

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3 417 climate response in their prey base. Although we did not test the relationship here, it is also  
4 418 possible that variation in wolf phenology may be sensitive to both the diversity of available prey  
5 419 species and the temporal changes in their availability.

7 420 Climatic drivers that affect kill rates during parturition for large carnivores, such as the  
8 421 availability and vulnerability of ungulates or the availability of alternative prey during the  
9 422 summer (e.g., fossorial mammals and Canadian beaver, *Castor canadensis*), may also be  
10 423 important to reproductive success (Frame *et al* 2008, Messier 1994, Vucetich *et al* 2002). Our  
11 424 results indicated that increased autumn precipitation decreased the odds of pup recruitment the  
12 425 following summer. Higher than average precipitation from late autumn through early spring,  
13 426 particularly in the form of snow, can contribute to reduced overwinter survival in many large  
14 427 ungulates, disproportionately affecting the most vulnerable age classes (Van de Kerk *et al* 2018,  
15 428 White *et al* 2011). Although this may provide a short-term benefit to carnivores in terms of  
16 429 elevated prey vulnerability during winter (Carroll 2007, Hebblewhite 2005, Metz *et al* 2012),  
17 430 particularly harsh over-winter conditions may precipitate sharp population declines in both  
18 431 ungulate (Hegel *et al* 2010a, Blackburn and Duncan 2001, Albon *et al* 2017, Vors and Boyce  
19 432 2009, Ims *et al* 2008) and non-ungulate prey (Morrison and Hik 2007, Patil *et al* 2013) the  
20 433 following summer, thereby reducing prey availability during the wolf pup-rearing period. The  
21 434 large, positive effect of PDO, for which positive cycles are commonly associated with larger  
22 435 northern ungulate populations (Hebblewhite 2005, Hegel *et al* 2010a, Joly *et al* 2011, Hegel *et al*  
23 436 2010b), and irruptions in rodent populations (Morrison and Hik 2007) which can serve as  
24 437 supplementary prey for wolves (Latham *et al* 2013, Gable *et al* 2018), provides further support  
25 438 for the possible role of prey abundance in determining reproductive success (White 2008).  
26 439 Similarly, as 'central-place' foragers during a period when young are stashed at pup-rearing sites  
27 440 and are relatively sedentary (Mills and Knowlton 1991, Frame *et al* 2008), we found that home  
28 441 range area during pup-rearing was negatively correlated with reproductive success, indicating  
29 442 wolf packs that needed to travel more during the summer months, presumably in search of food,  
30 443 were less successful. Of the remaining summer covariates, we found moderate support for  
31 444 reduced wolf reproductive success during hotter summers. As coursing predators during a period  
32 445 of the year with extended daylight, higher temperatures may reduce time spent hunting due to  
33 446 increased physiological stress akin to what has been observed in African wild dogs (*Lycaon*  
34 447 *pictus*; Woodroffe *et al* 2017). Although our results establish a clear link between climate and  
35 448 wolf reproductive ecology, we could not directly test these relationships due to lack of sympatric  
36 449 data on prey dynamics during our study period. A multi-trophic analysis of responses to climate  
37 450 variability would be a valuable next step to reveal mechanisms by which climate-induced  
38 451 phenological shifts impact higher trophic levels.

## 45 452 **Conclusions:**

46 453 Climate change is increasingly recognized as one of the major causes of species endangerment  
47 454 (Stanton *et al* 2015). Local and regional changes in climate have altered the phenology and  
48 455 distribution of plant and animal species across a range of ecosystems (Parmesan 2006). Range  
49 456 shifts (or contractions) and phenological advancements coincident with observed climate trends  
50 457 have occurred disproportionately across species within communities (Parmesan and Yohe 2003),  
51 458 contributing to the destabilization of species interactions including those between predators and  
52 459 prey (Ripple *et al* 2014, Parmesan 2006). Although there is a growing body of literature that  
53 460 suggests large carnivores may buffer communities and ecosystems against the detrimental effects  
54 461 of climate change (Wilmers and Getz 2005, Gormezano and Rockwell 2013, Ripple *et al* 2014),  
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3 462 few studies have investigated the direct impact of climate on large carnivore demography across  
4 463 a large geographic domain. Our results indicated that climate can interact with carnivore  
5 464 reproduction in complex and nuanced ways. We found no evidence indicating that advancing  
6 465 spring onset, nor the ability of individuals to synchronize denning with spring onset, was  
7 466 detrimental to wolf reproductive success, at least within the range of observed changes in  
8 467 climate. Although this would indicate carnivores are likely quite resilient to shifts in seasonality,  
9 468 we also found wolf reproductive success was sensitive to weather conditions that likely shaped  
10 469 the availability, vulnerability, and hunting success of large ungulates. Thus, carnivore persistence  
11 470 may depend on the ability of prey species to respond adaptively to weather conditions at local or  
12 471 regional scales and avoid destabilizing predator-prey dynamics (Visser *et al* 2004, Durant *et al*  
13 472 2007, Stenseth and Mysterud 2002). Future efforts to evaluate carnivore phenological response  
14 473 to climate signals would benefit from explicit consideration of the differential responses of  
15 474 predator and prey to climate dynamics. Doing so will help elucidate carnivore resilience under  
16 475 continued climate change as well as provide clarity on whether predators can serve as ‘climate  
17 476 buffers’ within communities through population regulation (Wilmers *et al* 2012).

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### 482 **Competing Interests**

483 All authors declare that there are no conflicts of interest in the publication of our findings.

### 484 **Data availability**

485 The data that support the findings of this study are openly available at the NASA ORNL DAAC:  
486 [URL and DOI forthcoming!]

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695 **Tables**

696 Table 1: The hypothetical mechanisms by which climate influences wolf denning phenology and reproductive success. These  
 697 hypotheses were used to justify the climate covariates used in each analysis.  $t-1$  indicates the season prior to the denning event.

Season	Mechanism	Predictions
<i>Denning phenology</i>		
Spring <sub><math>t-1</math></sub>	Past experience may inform spring onset the following year, particularly with strong correlation between past and current spring conditions.	Later SOS during the previous spring will promote later denning in the current year.
Summer <sub><math>t-1</math></sub>	Summer growing season conditions may influence female ungulate condition, timing of ungulate estrus, and overwinter wolf condition, potentially affecting wolf breeding phenology.	Longer and more productive growing seasons (LOS, tiNDVI), as well as higher temperatures, will promote earlier denning.
Autumn <sub><math>t-1</math></sub>	Autumn conditions influencing rut phenology in ungulates may cue wolf pair formation and breeding in the winter.	Lower temperatures and higher precipitation totals in the autumn will delay wolf denning.
Winter <sub><math>t-1</math></sub>	Winter conditions may affect the timing of pair formation/disruption and female condition in wolves, potentially driving the timing of estrus.	Lower temperatures and higher snow water equivalent (SWE) in the winter will delay wolf denning.
Decadal cycles	Longer term, regional climate patterns may influence prey populations states, influencing prey vulnerability and availability.	High snowfall years in PDO/AO cycles will delay wolf denning.
<i>Reproductive success</i>		
Autumn <sub><math>t-1</math></sub>	Autumn conditions affect the abundance and condition of prey from winter through pup rearing, thereby affecting female wolf body condition through the early stages of reproduction.	Higher Autumn temperatures with less precipitation will improve reproductive success.
Winter <sub><math>t-1</math></sub>	Winter conditions may influence prey availability and vulnerability, thereby affecting female wolf body condition through the early stages of reproduction.	More winter precipitation and higher snow water equivalent (SWE) will improve reproductive success.
Spring	Parturition phenology and synchrony with SOS may influence availability of vulnerable prey when caloric demands are highest for lactating mothers and developing young, thereby influencing wolf reproductive success.	Higher synchronicity between wolf denning and SOS will improve reproductive success.
Summer	Summer climatic conditions may influence prey abundance, availability, and susceptibility to predation. Temperatures and precipitation may influence time spent hunting in wolves as a coursing predator.	Longer, more productive growing seasons (LOS, tiNDVI) and cooler temperatures will improve reproductive success.

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2  
3 Decadal cycles

4 Longer term, regional climate patterns may influence prey  
5 populations states, influencing prey vulnerability and  
6 availability.

7 Warmer and wetter years in PDO/AO cycles will  
8 increase reproductive success.

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699 Table 2: The centroid location, number of pack-years (N), and monitoring periods used in an assessment of grey wolf denning  
 700 phenology and reproductive success partitioned by study.

<b>Study</b>	<b>Longitude</b>	<b>Latitude</b>	<b>Denning Phenology N</b>	<b>Reproductive Success N</b>	<b>Years</b>
Gwich'in NRB, NWT, CA	-135.76367	67.83620	3	3	2007 - 2007
Yukon-Charley Rivers NPP, Alaska, USA	-143.22796	65.04694	63	57	2003 - 2015
Denali NP, Alaska, USA	-150.48638	63.63523	85	76	2004 - 2016
ADFG Nelchina PUA, Alaska, USA	-146.81178	62.40836	10	7	2000 - 2005
Great Slave Lake, NWT, CA	-116.11118	60.88060	7	6	2016 - 2017
Lake Clark NP, Alaska, USA	-154.58120	60.49529	11	8	2009 - 2013
West Athabasca River, Alberta, CA	-112.96679	55.85988	8	5	2006 - 2007
Jasper-Banff NP, Alberta-BC, CA	-117.69928	52.97055	40	24	2000 - 2011

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702 Table 3: Variable descriptions for all covariates used in an assessment of wolf denning phenology and reproductive success. Values  
 703 represent summaries across all records, and therefore all study systems and years, within the complete dataset (i.e., reproductive  
 704 phenology dataset). The mean and standard deviations displayed here were used to standardize covariates prior to model fitting.

<b>Covariate</b>	<b>Full Name</b>	<b>Mean</b>	<b>Standard Deviation</b>	<b>Minimum</b>	<b>Maximum</b> <sup>705</sup>
Sync_SOS	Denning date synchrony with SOS (Days)	0.00	20.81	-59.47	43.45
SOS	Start of growing season (Day of Year)	137.88	14.70	101.95	177.31
tiNDVI	Time-integrated NDVI	12.04	3.10	4.36	31.49
LOS	Length of growing season (Days)	18.59	3.04	10.53	31.31
January_PDO	January Pacific Decadal Oscillation Index	0.18	1.12	-2.00	2.45
Annual_PDO	Annual Pacific Decadal Oscillation Index	-0.08	0.85	-1.29	1.63
January_AO	January Arctic Oscillation Index	-0.21	1.38	-2.59	2.03
Annual_AO	Annual Arctic Oscillation Index	-0.03	0.41	-1.04	0.63
Autumn_TMIN	Median autumn daily minimum temperature (°C)	-5.90	2.95	-14.00	0.00
Autumn_TMAX	Median autumn daily maximum temperature (°C)	1.48	3.30	-7.00	10.00
Autumn_PRCP	Autumn total precipitation (mm)	133.30	70.49	23.00	442.00
Winter_TMIN	Median winter daily minimum temperature (°C)	-18.68	5.41	-30.00	-8.00
Winter_TMAX	Median winter daily maximum temperature (°C)	-7.64	5.27	-23.00	3.00
Winter_SWE	Winter daily snow water equivalent	90.38	53.10	12.00	404.00
Summer_TMIN	Median summer daily minimum temperature (°C)	5.91	2.14	-3.00	11.00
Summer_TMAX	Median summer daily maximum temperature (°C)	17.35	2.75	11.00	24.00
Summer_PRCP	Summer total precipitation (mm)	257.23	94.96	44.00	518.00
SDD	Snow disappearance date (Day of Year)	125.76	16.47	94.00	232.00

706 Table 4: Top models ( $\Delta AICc < 2$ ) for each of three analyses evaluating the effect of climatic signals on grey wolf denning phenology  
 707 and reproductive success and the associated degrees of freedom (DF), the relative change in Akaike Information Criterion corrected  
 708 for small samples sizes ( $\Delta AICc$ ), and goodness-of-fit (concordance for phenology and conditional pseudo- $R^2$  for success). Model  
 709 weights are based on 2124 models in each analysis. Covariate names are described in detail within Table 3.

<b>Denning phenology</b>						
<i>Model</i>	<i>Model Coefficients</i>	<i>K</i>	<i>LL</i>	<i><math>\Delta AICc</math></i>	<i>Weight</i>	<i>Concordance</i>
1	Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO	5	-964.94	0.00	0.031	0.670
2	Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO	6	-964.10	0.44	0.025	0.670
3	tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO	5	-965.20	0.52	0.024	0.666
4	Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX	4	-966.30	0.63	0.022	0.661
5	tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO	4	-966.31	0.65	0.022	0.663
6	Annual_AO + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO	6	-964.55	1.35	0.016	0.671
7	Annual_AO + Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO	6	-964.59	1.42	0.015	0.673
8	Annual_AO + Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO	7	-963.63	1.63	0.014	0.675
9	Annual_AO + Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX	5	-965.77	1.66	0.013	0.666
10	Annual_AO + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO	5	-965.81	1.75	0.013	0.667
11	Autumn_PRCP + tiNDVI + Summer_PRCP + Summer_TMAX + Winter_TMAX + Annual_PDO	6	-964.78	1.80	0.012	0.669
12	Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX	5	-965.85	1.82	0.012	0.663
13	tiNDVI + Summer_PRCP + Summer_TMAX + Winter_TMAX + Annual_PDO	5	-965.86	1.85	0.012	0.663
14	Autumn_PRCP + Autumn_TMAX + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO	6	-964.82	1.89	0.012	0.669
15	tiNDVI + Summer_PRCP + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO	6	-964.87	1.97	0.011	0.665
16	Null	0	-991.83	43.52	0.000	0.500
<b>Reproductive success</b>						
<i>Model</i>	<i>Model Coefficients</i>	<i>K</i>	<i>LL</i>	<i><math>\Delta AICc</math></i>	<i>Weight</i>	<i>Cond. <math>R^2</math></i>
17	HR_Area + Autumn_PRCP + Summer_TMAX* + Annual_PDO	7	-94.02	0.00	0.036	0.216
18	HR_Area + Autumn_PRCP + Summer_TMAX* + Winter_SWE + Annual_PDO	8	-93.22	0.58	0.027	0.243
19	HR_Area + Autumn_PRCP + tiNDVI + Summer_TMAX* + Annual_PDO	8	-93.31	0.75	0.025	0.224
20	HR_Area + Autumn_PRCP + Summer_TMAX* + Winter_TMAX + Annual_PDO	8	-93.35	0.85	0.023	0.236



21	HR_Area + Autumn_PRCP + Summer_TMAX* + Winter_SWE + Winter_TMAX + Annual_PDO	9	-92.42	1.20	0.020	0.265
22	HR_Area + Autumn_PRCP + tiNDVI + Summer_TMAX* + Winter_SWE + Annual_PDO	9	-92.49	1.33	0.018	0.248
23	HR_Area + Autumn_PRCP + tiNDVI* + Summer_TMAX* + Annual_PDO	8	-93.76	1.66	0.016	0.213
24	HR_Area + Autumn_PRCP + tiNDVI* + Summer_TMAX* + Winter_SWE + Annual_PDO	9	-92.70	1.75	0.015	0.245
25	Null	3	-106.20	15.85	0.000	0.089

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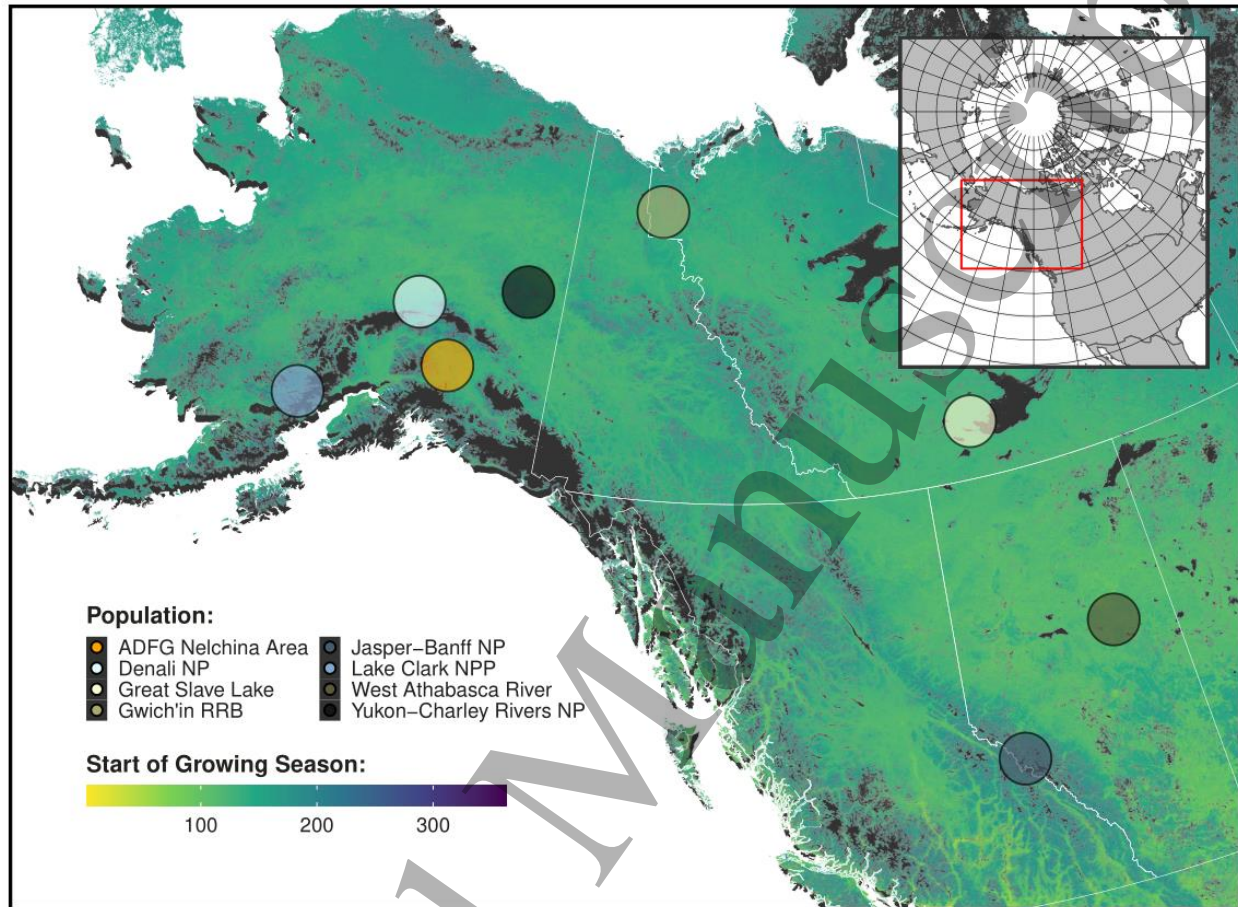
711 Table 5: The parameter weights, model-averaged estimates, and confidence intervals (L85: lower  
 712 85% confidence limit, U85: upper 85% confidence limit) for each coefficient considered within  
 713 three distinct analyses evaluating the effect of climatic signals on grey wolf denning phenology  
 714 and reproductive success. Coefficient and confidence interval estimates were derived from  
 715 standardized covariates and unconditional standard errors, respectively. As time-to-event models,  
 716 negative coefficients indicate later denning and vice versa.

<b>Coefficient</b>	<b>Parameter Weight</b>	<b>Estimate</b>	<b>L85</b>	<b>U85</b>
<i>Denning phenology</i>				
Winter_TMAX	1.00	0.34	0.20	0.48
Summer_TMAX	0.98	0.30	0.16	0.45
tiNDVI	0.94	-0.32	-0.47	-0.17
Annual_PDO	0.64	-0.14	-0.26	-0.03
Fall_PRCP	0.57	-0.14	-0.27	-0.01
Winter_SWE	0.46	-0.10	-0.21	0.01
Annual_AO	0.38	-0.08	-0.18	0.03
SOS <sup>a</sup>	0.32	0.10	-0.16	0.35
Summer_PRCP	0.30	0.04	-0.11	0.19
Fall_TMAX	0.28	0.05	-0.11	0.20
LOS	0.28	-0.01	-0.20	0.22
<i>Reproductive success</i>				
Fall_PRCP	0.90	-0.61	-0.96	-0.27
Summer_TMAX <sup>b</sup>	0.88	-0.68	-1.05	-0.32
Annual_PDO	0.75	0.49	0.18	0.80
HR_Area	0.70	-0.54	-0.93	-0.16
Winter_SWE	0.35	-0.26	-0.54	0.02
Winter_TMAX	0.32	0.30	-0.07	0.67
tiNDVI	0.30	-0.34	-0.71	0.03
Summer_PRCP <sup>b</sup>	0.24	0.23	-0.21	0.68
Den match with SOS	0.24	0.20	-0.16	0.57
tiNDVI <sup>b</sup>	0.19	-0.24	-0.59	0.12
Fall_TMAX	0.18	-0.03	-0.37	0.30
Annual_AO	0.17	-0.02	-0.31	0.27

717 <sup>a</sup>Measured the previous year

718 <sup>b</sup>Measured the summer after denning.

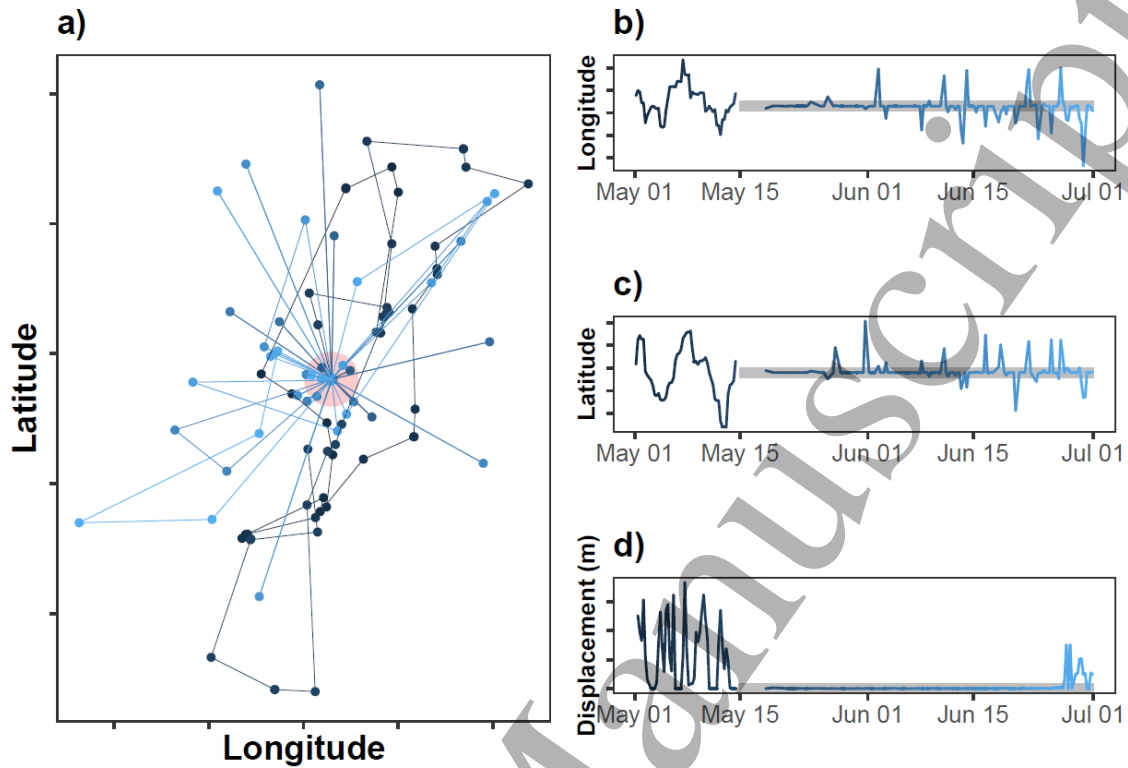
719 **Figures**  
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721

722 *Figure 1.* Spatial distribution of eight wolf study populations used in an assessment of denning  
723 phenology in response to climate signals (2000 – 2017). The base map shows the day of year  
724 representing the NDVI-derived start of growing season in 2010.

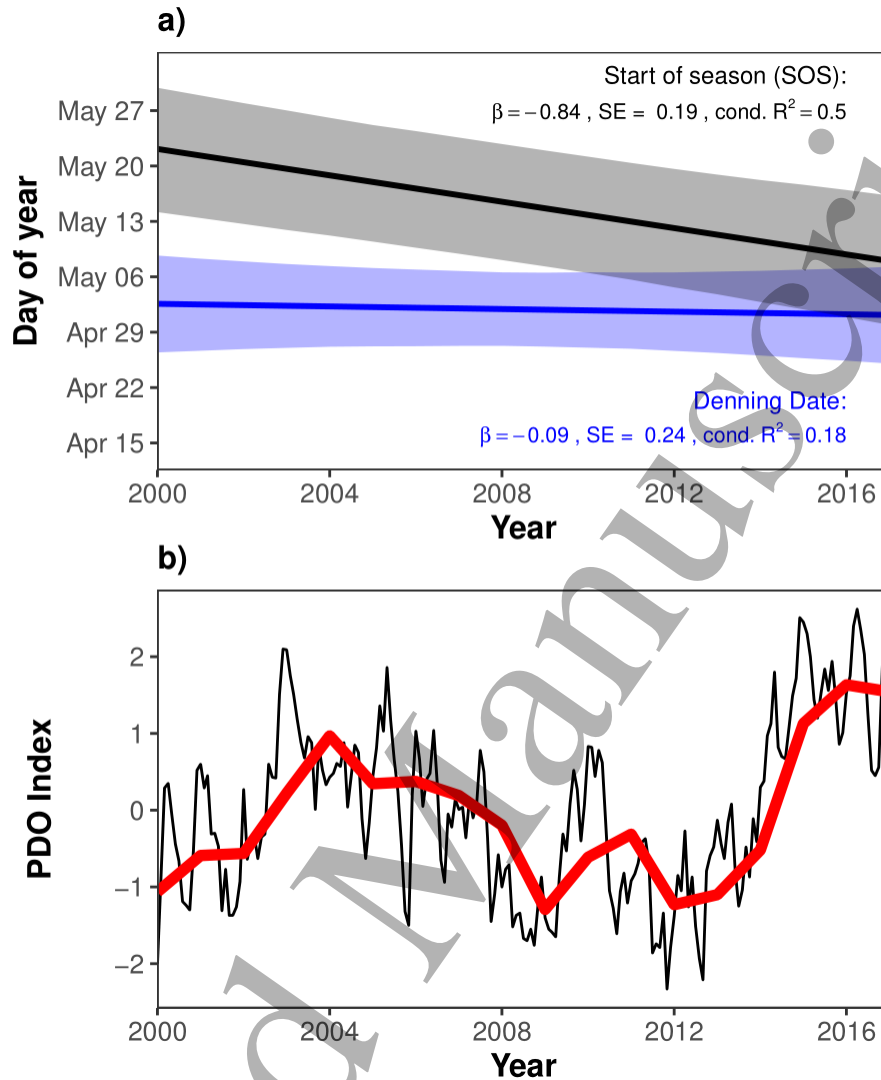
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726 *Figure 2.* A visual depiction of the approach used to characterize wolf den and rendezvous sites  
 727 using a combination of spatial clustering and confined median daily displacements. Each point  
 728 (a) and line (a-d) correspond to a median daily location and displacement between consecutive  
 729 locations, respectively, for a single reproductive female. All points and displacements are  
 730 colored by time from dark blue (early) to light blue (late). The red circle in (a) indicates a den  
 731 site with characteristic web-like movements. The gray semi-opaque band in (b-d) highlights the  
 732 timing and duration of an individual's denning activity. Further, the 4-day gap in locations  
 733 depicted at the start of the denning period was due to the collars inability to acquire satellite  
 734 signals when in a den, often a tell-tale for den initiation in collared females.

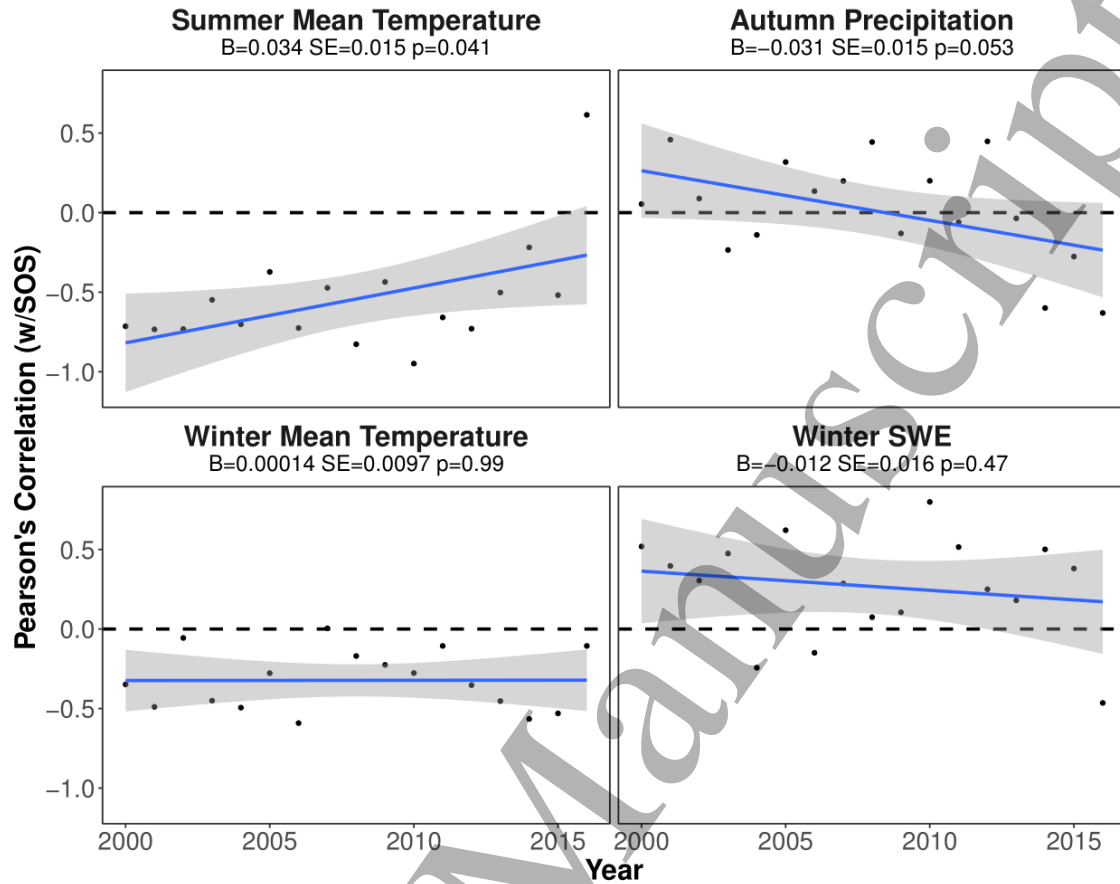
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736 *Figure 3.* Linear regression model fit for start of growing season (SOS, black line with gray 95%  
 737 CI band) and marginal denning date (all populations, blue line and 95% CI band) (a). The PDO  
 738 index (b) plotted as monthly means (black line) and annual means (red) during the study period  
 739 (2000 - 2017).

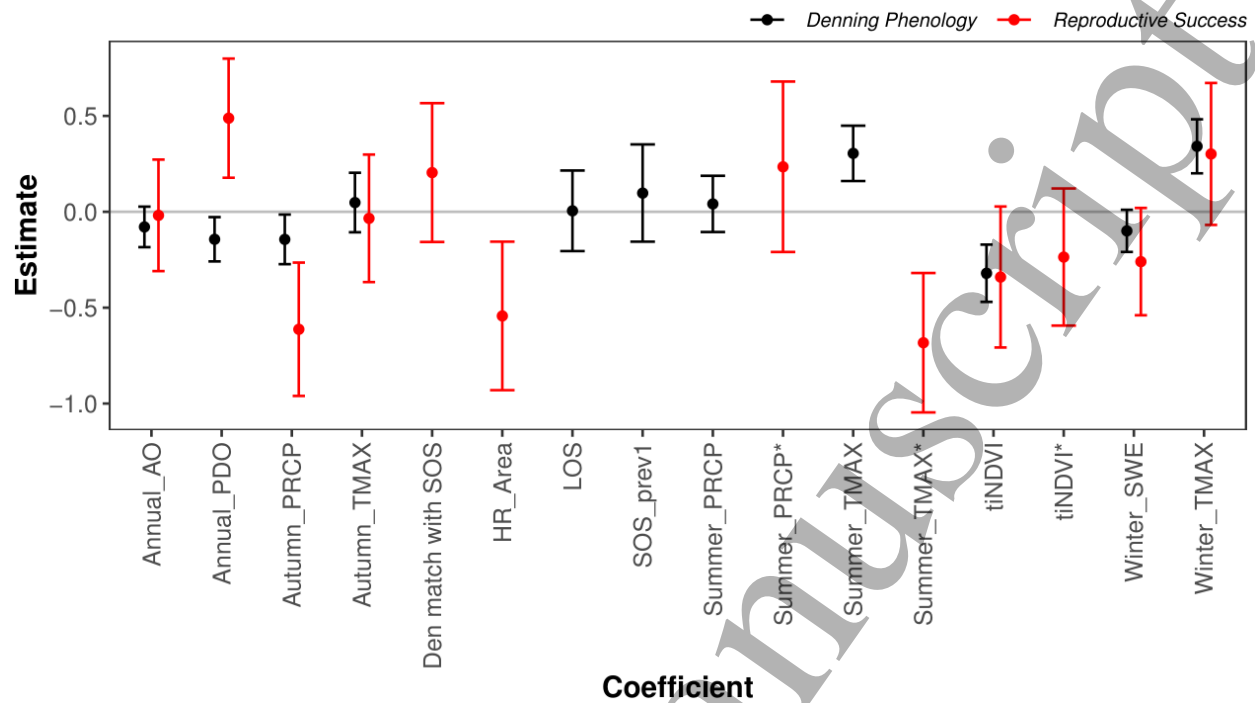
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741 *Figure 4.* Panels showing the temporal trends in Pearson's correlation coefficients between start  
 742 of growing season (SOS) and each local climate metric from the preceding season paired by  
 743 study population. Each point estimate reflects a single pairwise correlation coefficient for all  
 744 eight study populations in a given year. The purpose is to highlight the potential for preceding  
 745 seasonal conditions to cue spring onset and may indicate to what extent species can depend on  
 746 these metrics as indicators of future conditions.

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Coefficient

748 *Figure 5.* Coefficient plots for all model averaged coefficients in an assessment of gray wolf  
 749 denning phenology (black; Cox proportional hazard regression) and reproductive success (red;  
 750 generalized linear mixed model). Coefficients with a '\*' indicate covariate measurements that  
 751 were made during the denning period. All remaining coefficients were derived from  
 752 measurements made during seasons preceding the denning period. Error bars represent 85%  
 753 confidence intervals derived from unconditional standard errors.

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